FURTHER STUDIES ON HYDROMYZA CONFLUENS LOEW, (DIPTERA).*

By Paul S. Welch

INTRODUCTION

In a previous paper ('14), the writer reported the results of some observations on *Hydromyza confluens*, an aquatic dipterous insect which occurs abundantly about Douglas Lake, Northern Michigan. Parts of two seasons have since been spent in the same region and additional data, as well as confirmation of previously recorded observations, have been secured. The new material incorporated in this paper not only aids in completing our knowledge of the life history of this form but also throws new light on the interesting adaptations already described.

THE EGG

Description.—When first laid, the eggs (Figs. 1–2) are uniformly white, with a very slight tint of yellow. In clear, quiet water, they are usually more easily seen when submerged on the yellow water-lily petiole than when the latter is lifted from the water. They are elliptical in lateral view and subcylindrical (Fig. 3) in transverse section. A large number of eggs, removed from the petioles and measured, had an average length of 1.69 mm., the extremes being 1.54 and 1.76 mm. respectively. The maximum diameter, which is in a region well towards the more acute end, has an average length of 0.35 mm., the extremes being 0.30 and 0.40 mm. The ends differ distinctly in shape, one being bluntly pointed while the other is more rounded and is characterized by a depression in the apex. A straight, longitudinal, acute carina extends from end to end, occupying the mid-position in a deep, broad, longitudinal fossa, dividing it into two similar parts. This divided fossa comprises almost one-third of the periphery and is bounded laterad by two other longitudinal carinæ which extend almost parallel to the median carina, converging and uniting at the ends of the egg. The effect of this fossa is to give the egg a flat appearance on one side. Superficially, the chorion is smooth except in the region of the longitudinal fossa. The mid-longitudinal carina bears on its sides numerous minute, conical spines (Fig. 5). Similar minute projections occur on and near the vertex of each lateral, longitudinal carina. These minute processes are produced by an extra development of some of the columnar exochorionic units. The chorion is approximately uniform in thickness in all parts of

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the egg-capsule except at the carinæ and in the depressions between them where it is distinctly thicker. The average thickness is about 0.0048 mm. The exochorion and endochorion are distinct, all variations in thickness being confined to the former which is composed in part of very minute, closely set, columnar units. For the greater part of its length, the median carina has an acute crest (Fig. 3) but near the ends it gradually merges into a lower ridge whose crest is broad and slightly rounded.

Under magnification, the surface of the chorion, except the region including the longitudinal carinæ and fossa, appears faintly but definitely reticulate, being composed of polygonal units (Fig. 4) which vary somewhat in shape and size but are usually hexagonal and more elongated in the direction of the long axis of the egg. Their average surface dimensions are about 0.112 and 0.056 mm. They contain numerous, minute, circular, uniformly distributed structures which give to the surface a granular appearance. These structures are of uniform size and appearance and are never contiguous. Structurally, they seem to be the ends of the columnar units which compose a great part of the chorion. Exclusive of the fossa and carinæ, they are present over the entire surface of the egg, being absent only on the narrow, homogeneous zones which separate the hexagonal areas.

Oviposition has not been observed and the writer has failed to secure eggs from females placed in the aquaria with food plants for that purpose. The identification of the egg has been made from a comparison with fully developed eggs dissected from females. The characteristic size, shape, and external structures, such as the carinæ, fossæ, and hexagonal areas, and a microscopical comparison of transverse sections of the eggs leave no doubt as to their identity. In addition, the writer secured a large number of eggs in various stages of development on the petioles of the water-lily and demonstrated the fact that the resulting larvæ develop the characteristic effect on the petiole, ultimately producing adults of *H. confluens*.

In connection with the dissection of females for developing eggs, it was noticed that, as in many other insects, there is a definite relation between the position of the egg in the ovariole and the shape of the completely formed egg. The larger, more pointed end is nearer the oviduct while the smaller, blunter end, which is characterized by a small terminal concavity, is nearer the terminal filament. It is then possible to determine accurately in the egg already deposited what was the previous relation to the reproductive organ.

Place and Method of Deposition.—The eggs are deposited singly at irregular intervals on the surface of the floating leaf petioles of the yellow water-lily (*Nymphœa americana* (Provancher) Miller & Standley). No eggs were found on the petioles of the submerged leaves and none were observed on other aquatic plants occurring in the vicinity of the yellow

water-lily beds. None were found on the petioles or other parts of the white water-lily (*Castalia odorata*) although both species of water-lily intermingle in the same beds. This restriction of the eggs to *N. americana* accounts for the constant relation of the larval and pupal stages to the same plant which is discussed in the earlier paper (Welch, '14, p. 136). Apparently, the female has the ability to recognize the food-plant even in the presence of numerous other aquatic plants, some of which present conditions similar to those of *N. americana* and are closely related to it.

Oviposition is constant with respect to the following features: (1) The long axis of the egg is parallel to the long axis of the petiole. (2) The surface of the egg in contact with the petiole is always opposite the carinæ and fossa. (3) The blunt end of the egg is directed towards the rootstalk and the acute end towards the leaf.

Eggs may occur anywhere from the leaf attachment to the rootstalk, even on petioles almost six feet long. As many as seventeen were found on a single petiole, scattered over a length of only one and one-half feet. An examination of a large number of petioles showed that while eggs are deposited on both the plane and convex surfaces, by far the greater number occur on the latter. The significance of this decided preference of the female in selecting the position of the egg is not known. The egg is rather firmly fixed to the surface of the petiole, apparently by a small amount of sealing fluid which accompanies the egg at oviposition. As will be shown later, the position of the egg determines the future position of the larva and pupa in the petiole.

As stated above, oviposition has not been observed and it is not known whether the eggs which occur on a single petiole are deposited by a single female or by several females. In the earlier paper, the writer ('14, pp. 138–139) called attention to the small variation in the maturity of the larvæ and pupæ and suggested that possibly the eggs on a given petiole were deposited at the same time by a single female. While this is still an open question, counter-evidence was apparently secured when, in the dissection of the ovaries of a considerable number of females, collected during the time when eggs were appearing in the field, it was found that no individual contained more than

nine approximately mature eggs at a time, the other eggs in the ovaries being distinctly undeveloped. It thus seems impossible for a female to deposit more than nine eggs during a single trip below the surface of the water, assuming that she could withstand submergence long enough to deposit the already mature or almost mature eggs, and it scarcely seems possible that the sojourn below could be so long that undeveloped eggs would have time to mature and be deposited also. Therefore, it seems improbable that, in instances where as many as seventeen eggs were found on a single petiole, all of them could have been deposited at one time by the same female. It is true, as pointed out, that the difference in the maturity among the larvæ or pupæ on a single petiole is often not marked but it may be that such a condition is due to the coincidence of the egg-laying period of a large number of females in that particular locality, a possibility which is borne out by the observation that in the region studied during the past five summers it often happened that many adjacent petioles contained larvæ of approximately the same degree of development.

Development of Eggs.—Owing to the fact that the writer was not able to secure the deposition of eggs in the laboratory, the egg period is not definitely known. Collections of eggs showing the least development were secured in the field, brought to the laboratory, kept under approximately natural conditions, and the last hatching dates recorded. This imperfect evidence points to an egg period of about six to eight days. The only noticeable external change which accompanies the development of the egg is a darkening of the color which begins to appear only a few hours before hatching.

Not only does a definite and constant relation exist in the position of the ends of the egg in the ovariole, but a similar relation exists in the orientation and development of the larva within the egg. The anterior end of the larva is invariably developed in the rounded, blunt, concave end, i. e., the one which is nearest the terminal filament while still within the ovariole. Furthermore, in all of the specimens examined, the ventral part of the larva is developed on the side opposite the carinæ and the dark, conspicuous mouth armature is curved in the same direction.

THE LARVA

Process of Hatching.—The place of emergence of the larva from the egg is a constant feature. The larva makes an exit hole through the egg capsule near the blunt, concave end, on the side next to the petiole. The position of the exit hole is determined by the position of the larva and is directly in front of the chitinous mouth armature, which, no doubt, is the instrument by means of which the opening through the shell is made. The exit hole is usually more or less circular in outline and somewhat larger than is necessary for the passage of the body of the larva. Occasionally, hatched eggs show a more extensive breaking down of the chorion next to the petiole. The larva bores directly into the petiole and there passes its entire existence. No evidence whatsoever was observed of any preliminary wandering of the larva after emergence from the egg. The latter always marks the position of the future abode of the resulting larva and pupa.

Recently Hatched Larva.—On emergence from the egg, the larva is milk-white in color, with the exception of the black mouth armature and the blackish caudal projections. The body (Fig. 6) is cylindrical, elongate, slender, and smooth. Measurements, made on living, recently hatched specimens, show a rather constant length of from 2.33 to 2.5 mm. The maximum diameter, in the region of the future thoracic segments, is approximately 0.29 mm. Intersegmental grooves are distinct but shallow. The anterior end of the body is rather bluntly rounded and shows no special structures, except the emergent teeth of the mouth armature. Posteriorly, the body is distinctly tapering and terminates in a pair of acute chitinous projections which bear the terminal spiracles. The integument is covered with very fine, pointed, conical projections. They are uniform in size and shape over the body except on the anterior margin of the first thoracic segment where they are a little more distinct. In most specimens, the translucency of the body allows the principal trunks of the tracheal system to stand out clearly. Two main, longitudinal tracheæ extend, one on each side, from the above-mentioned caudal, pointed, chitinized projections to the anterior region of the body, near the internal end of the mouth armature, where each divides into three branches. The finer details of this system have not been worked out.

Development of the Larva.—No striking external changes accompany the development of the larva. It increases in length and becomes somewhat more robust in proportion to the length. The yellowish tint in the color of the body becomes a little more apparent, the general body-surface smoother, and the intersegmental grooves less broad and deep, although they continue to be distinct. The larval period has not been accurately determined and no statement can be made at this time as to the rate of development.

The Relation to the Petiole.—Needham ('08), in describing the relation of the immature stages of *H. confluens* to the food-plant, designated the ultimate effect on the petiole as a *gall.* This same form of designation was followed by the writer ('14) in his first paper on this insect. However, subsequent work led to the investigation of the problem of whether the action of the larva on the petiole results in the production of a true gall or whether the superficial appearance of the infested petiole is merely a case of gall resemblance. Attention was called in the writer's earlier paper ('14, p. 137) to the observation that not all infested portions of the petioles showed swellings and often the diameter was not increased at all.

Specimens of the so-called galls were secured in all stages of development and sections of the same were made with the view of determining whether the growing larva produced any change in the character of the plant tissue in its immediate vicinity. An examination of these sections and a careful comparison with similar sections of the normal petiole showed that no change in the surrounding tissue occurs, that the relation of the larva to the petiole is merely one of simple interior excavation of the latter by the former and that the increase in diameter which sometimes appears is due to foreign accumulations within. The only change which was detected in the tissues was a brownish discoloration of the cells which bound the cavity made by the larva. Since the term gall is properly restricted to an abnormality in plants in which the causative factor leads to the development of tissues that differ from the normal ones, it becomes evident that the immature stage of *H. confluens* does not produce a true gall and that the occasional ovoid swelling of the petiole is not the result of an excrescence.

THE ADULT

In the writer's earlier paper ('14), a number of observations on the habits and activities of the adults were presented, and subsequent studies have yielded data which are confirmatory of the same. In addition, a few new data were secured which seem worthy of record.

Food Habits.—The relation of these flies to the yellow water-lily has been discussed somewhat in detail in the above-mentioned paper (pp. 145–147) and the possibility of nectar being produced by the flowers of *N. americana* and serving as a food for these insects was pointed out. This matter is still in doubt but the behavior of the flies in the flowers offers circumstantial evidence in favor of such a conclusion. However, it appears that the flies have other means of solving the food problem. Adults were repeatedly observed feeding on the exposed tips of the stamens. In most cases, this behavior was too long continued to be interpreted as a mere random inspection or testing of the stamen surface. The character of the food secured from the tips of stamens is not known. Possibly the pollen serves as food. Occasionally, flower stalks were, by different mechanical agents, broken off above water and partly stripped down, exposing a broken end on which an exudation of the liquid substances of the plant occurred. Flies often gathered in considerable numbers on such broken stalks and fed there for long intervals.

It also appears that these flies do not confine their feeding activities wholly to the yellow water-lily. Occasionally, adults of *Chironomus* sp. were found dead on the water-lily leaves and many of them, in the process of rapid disintegration, were discovered by these flies, the latter clustering about the dead insects and performing feeding movements. The evidence seemed conclusive that the flies were feeding on the juices of the dead insect. A number of experiments were tried by securing the bodies of *Chironomus* sp. and, after allowing them to lie in water for several hours, they were placed on the water-lily leaves where the adults of *H. confluens* were abundant. It was shown in this way that the dead insects had a distinct attraction for the flies, the latter seeking them rather quickly and definitely when not too remote from them. This response was so definite that the writer used the dead insects as a trap for the flies, thus facilitating the collection of the latter.

Light Relations.—No attempt has been made to carry on refined experiments on the behavior of these flies. However, observations and some rough field experiments were made on the relation of *H. confluens* to light, the results of which will be given in brief form.

A study of the habits of these flies in the field has shown that they are active during the day and are found in large numbers on the upper surfaces of the floating water-lily leaves. Very few were observed in any other situation. It thus appears that since the water-lilies grow in maximum exposure to sunlight and are never shaded, the flies prefer well-lighted conditions and positive phototaxis is suggested. A number of experiments were made by placing various lots of flies in a glass tube, closed at both ends and equipped with a close-fitting cover of heavy, black paper which enveloped about one-half of the length of the tube, other conditions remaining unchanged. By placing this tube in various positions with reference to the light and reversing it after certain intervals of time, the reactions of the insects could be noted. Irrespective of the position of the tube, the flies reacted positively to the light by seeking actively the uncovered end of the tube. These tests were repeated many times with the same results. The migration from one end of the tube to the other as the latter was reversed was continued over and over again without any appreciable change in the character of the response. Frequent use was made of this response in the collection of flies for other purposes and in the transference of individuals from one vial to another or from one breeding jar to another. While no experiments were carried on in order to determine whether any difference exists in the reaction by the different sexes, collections of flies from the top surfaces of the water-lily leaves, taken at random, showed no noteworthy difference in the number of males and females.

In the earlier paper, the writer ('14, p. 144) pointed out the probable method of oviposition by the female, namely, passage into the water on the under surface of the leaf and down the petiole to the places where the eggs occur. The discovery of the eggs makes this assumption all the safer. It thus appears that although the female is distinctly positive in reaction to light, this positive phototaxis is overcome by the stimuli inducing oviposition since the passage into the water is accompanied by a reduction of the light. Furthermore, the positive reaction to

light seems also to be overcome by the attraction to food since large numbers of the flies have been found on numerous occasions crowded into but slightly opened flowers of the yellow water-lily, the interiors of which were dark.

Distribution.—Attention has already been called (Welch, '14, p. 140) to the peculiar local distribution which was so marked in the Douglas Lake region. The observations of two additional seasons show that such a distribution is practically the same from year to year. Observations in other localities where *H. confluens* occurs would be of interest in this connection.

Thus far, *H. confluens* seems to have been reported only from Canada, Michigan, and New Jersey. However, there is reason to believe that it is more widely distributed than these meager data would indicate. While making a very hasty examination (June 27, 1915) of the life of the protected bays of Cedar Point, near Sandusky, Ohio, the writer found this fly, in the adult stage, in some abundance on the leaves and in the flowers of the yellow water-lily. None of the immature stages were found but this failure was due, no doubt, to the very superficial examination, lack of time preventing a thorough survey of the situation. Both sexes were present and several pairs were observed in copulation. Individuals collected at that time were bearing the pollen of the yellow water-lily and a few specimens almost completely covered with pollen were taken from the flowers. Evidently they were playing an active part in the cross pollination of these plants. Fulton ('11, p. 300) states that he found a number of flies visiting the yellow water-lilies, "*Nymphæa advena*," about Cedar Point but the particular species are not designated and his paper contains only a list of the Stratiomyidæ. Bembower ('11) studied the insect-pollinated plants of the Cedar Point region and while it was found that Diptera were collected in connection with *N. advena*, the different species are not indicated.

SUMMARY

1. Further studies on *Hydromyza confluens* in the vicinity of Douglas Lake, Michigan, confirm observations previously reported and yield new data on life history and behavior.

2. Eggs are deposited singly and irregularly along the submerged petioles of the floating leaves of the yellow water-lily (*Nymphæa americana*). Oviposition apparently does not occur on other plants.

3. The egg has certain definite and invariable external characters which facilitate identification, viz., the dissimilarity of the two ends, and the large, longitudinal fossa divided by the longitudinal carina.

4. Certain constant features with respect to the orientation and oviposition were noted: (a) In the ovariole, the blunt, concave end of the developing egg is nearest the terminal filament. (b) On the petiole, the blunt end is directed towards the root-stalk. (c) The long axis is parallel to the long axis of the petiole. (d) The side of the egg opposite the fossa and carina is in contact with the petiole. (e) The anterior end of the larva is developed in the blunt, concave end of the egg. (f) The ventral part of the larva appears to invariably develop on the side opposite the carina.

5. Incomplete evidence indicates that the occurrence of more than 7–9 eggs on a single petiole is due to oviposition by two or more females.

6. The position of the egg invariably marks the future position of the so-called "gall."

7. Microscopic examination of infested portions of the petioles shows that a true gall is not formed, the result being due to mere interior excavation.

8. In addition to the possible production of nectar by *N. americana* and its use as food, the adults were observed feeding: (a) on the exposed tips of stamens, possibly consuming the pollen; (b) on the exudation of broken, emergent flower stalks; and (c) on the dead bodies of certain insects (*Chironomus* sp.).

9. Field observations and experiments indicate that the adults exhibit a distinct, positive reaction to sunlight. It appears, however, that this positive phototaxis is overcome by the stimuli inducing oviposition and by the stimuli inducing the search for food.

10. Adults of *II. confluens* were collected about the yellow water-lily beds at Cedar Point, near Sandusky, Ohio, and evidence pointed to them as active agents in the cross pollination of these plants in that locality.

LITERATURE CITED

Bembower, W. 1911. Pollination Notes from the Cedar Point Region. The Ohio Naturalist, 11:378–383.

Fulton, B. B. 1911. The Stratiomyidæ of Cedar Point, Sandusky. The Ohio Naturalist, 11:299–301.

Needham, J. G. 1908. Notes on the Aquatic Insects of Walnut Lake. Appendix III. A Biological Survey of Walnut Lake, Michigan, by T. L. Hankinson. A Report of the Biological Survey of the State of Michigan, published by the State Board of Geological Survey as a part of the Report for 1907, pp. 252–271.

Welch, P. S. 1914. Observations on the Life History and Habits of Hydromyza confluens Loew, (Diptera). Ann. Ent. Soc. Am., 7:135–147.

EXPLANATION OF PLATE III

Fig. 1. Outline of egg showing surface which bears fossa and carinæ.

Fig. 2. Outline of egg showing shape when viewed ninety degrees from position indicated in Fig. 1.

Fig. 3. Egg capsule as it appears in transverse section.

Fig. 4. Camera lucida drawing of reticulation which appears on surface of egg capsule.

Fig. 5. Transverse section of median carina of egg.

Fig. 6. Recently hatched larva.